



TITLE:

Ontogeny of swimming speed, schooling behaviour and jellyfish avoidance by Japanese anchovy *Engraulis japonicus*.

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CITATION:

Masuda, R. Ontogeny of swimming speed, schooling behaviour and jellyfish avoidance by Japanese anchovy *Engraulis japonicus*. *Journal of fish biology* 2011, 78(5): 1323-1335

ISSUE DATE:

2011-04-04

URL:

<http://hdl.handle.net/2433/197318>

RIGHT:

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1 **Ontogeny of swimming speed, schooling behaviour and jellyfish avoidance by**

2 **Japanese anchovy *Engraulis japonicus***

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8 Running headline:

9 Ontogeny of anti-predator behavior in anchovy

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The ontogeny of swimming speed, schooling behaviour and jellyfish avoidance was studied in hatchery-reared Japanese anchovy *Engraulis japonicus* to compare its life history strategy with two other common pelagic fishes, jack mackerel *Trachurus japonicus* and chub mackerel *Scomber japonicus*. Cruise swimming speed of anchovy increased allometrically from 1.4 to 3.9 folds of standard length per second ($L_S \text{ s}^{-1}$) during the course from early larval to metamorphosing stage. Burst swimming speed also increased from 6.1 to 28 $L_S \text{ s}^{-1}$ in these stages. Cruise speed was inferior to that of chub mackerel, as was burst speed to that of jack mackerel. Anchovy larvae were highly vulnerable to predation by moon jellyfish *Aurelia aurita* and were readily eaten until they reached 23 mm L_S , but not at 26 mm L_S . Schooling behavior (indicated by parallel swimming) started at about 17 mm L_S . Average distance to the nearest neighbour was shorter than values reported in other pelagic fishes. The relatively low predator avoidance capability of Japanese anchovy may be compensated for by their transparent and thus less conspicuous body, in addition to their early maturation and high fecundity.

Key words: *Aurelia aurita*; behavioural ontogeny; Engraulidae; population dynamics; predator avoidance; shoaling.

INTRODUCTION

The world's largest fisheries have largely depended on clupeoids such as sardine *Sardinops* spp., herring *Clupea* spp. and anchovy *Engraulis* spp. (Hunter, 1980), among which anchovy are now probably the most dominant in many temperate areas. Periods of increased anchovy populations coincide with the declines of sardine populations off Japan, California, Peru and Chile (Chavez *et al.*, 2003). In the case of Japanese coastal waters, three major pelagic fishes, i.e., chub mackerel *Scomber japonicus* Houttuyn, jack mackerel *Trachurus japonicus* (Temminck & Schlegel), and Japanese anchovy *Engraulis japonicus* (Houttuyn), filled the empty niche resulting from the collapse of sardine *Sardinops melanostictus* (Temminck & Schlegel) populations in the late 1980s. Dominance of one or two of these species occurs at *c.* 10-year intervals (Matsuda *et al.*, 1991). Takasuka *et al.* (2008) studied the optimum spawning temperature of these fishes and found that *Sardinops melanostictus* and *Scomber japonicus* are stenothermal species with peak spawning at 16° C and 18° C, respectively, whereas *Trachurus japonicus* and *Engraulis japonicus* are eurythermal with optimum spawning at *c.* 22° C. This is coincident with the theory that fluctuations in pelagic fish populations are governed by global climatic change, the so-called “regime shift theory” (Kawasaki, 1992). Yet at each stage of population replacement, it is still not clear what would be the direct cause of mortality leading to the competitive advantage for any one species. It is necessary to elucidate which species will benefit from certain environmental conditions in order to better understand this cyclic pattern of population dynamics.

On the other hand, the population of anchovy *Engraulis encrasicolus* (L.) in the Black Sea has been seriously depleted over the past two decades in part due to predation by a gelatinous predator, an alien ctenophore, *Mnemiopsis leidyi* (Agassiz), that invaded in the 1980s (Shiganova, 1998). Castro et al. (2000) also found an apparent inverse relationship between the anchovy *Engraulis ringens* Jenyns larval density and gelatinous predators (medusae, ctenophores and siphonophores) off Chile. Because recently jellyfish blooms have become ubiquitous phenomena (Purcell *et al.*, 2007), anchovy and other pelagic fish populations may decline due to the increased predation and competition.

Ecological aspects of pelagic fishes have been intensively studied by using otolith analysis of wild collected specimens (*e.g.* Takahashi & Watanabe, 2005; Takasuka *et al.*, 2007). Survival in the wild, however, is the outcome of the combination of predation pressure and growth, both dependent on temperature and other environmental factors. However, an experimental approach using hatchery-reared fish may allow insights into differences in biological performance such as growth and behavior, as have been conducted on Atlantic herring *Clupea harengus* L. (Hunter, 1972), northern anchovy *Engraulis mordax* Girard (Blaxter, 1985) and red drum *Sciaenops ocellatus* (L.) (Fuiman *et al.*, 1999).

The goal of the present work was to collect basic information related to the ontogeny of anti-predator behaviour such as swimming speed, responsiveness, jellyfish avoidance and initiation of schooling behaviour in *Engraulis japonicus*. Masuda (2006) reported that among common pelagic fishes *Scomber japonicus* is an exceptionally fast

grower with a faster cruise swimming speed compared to *Trachurus japonicus* whereas *T. japonicus* has a fast burst swimming speed and has a high avoidance capability from moon jellyfish *Aurelia aurita* (L.). In the present work, equivalent data for *E. japonicus* were collected to conduct interspecific comparisons among these three species.

MATERIALS AND METHODS

HUSBANDRY OF BROODSTOCK AND HATCHERY PRODUCTION

Candidates of broodstock were obtained at a commercial set net operated by local fishermen in Tai, Maizuru, Kyoto (35° 56′ N, 135° 45′ E) on 15 May 2007. About 200 adult *E. japonicus* were collected from the catch, kept in two 70 l-containers, transported to the Maizuru Fisheries Research Station (MFRS) of Kyoto University and stocked in a broodstock tank (4 m in diameter, 30 m³ of sea water). Mean \pm S.D. standard length (L_S) of sub-sampled males ($n = 17$) and females ($n = 13$) were 100.8 ± 6.8 mm and 101.1 ± 8.9 mm, and their gonado-somatic index ($I_G = 100 \times (\text{gonad weight}) \times (L_S)^{-1}$) were 1.50 ± 1.24 and 1.26 ± 0.99 , respectively. Filtered seawater was provided in the broodstock tank. They were fed with *c.* 100 g of defrosted krill twice daily until satiation. First spawning was confirmed at 20.2° C on 13 June. Spawning continued until mid August. The highest number of eggs spawned per day was 350,000 recorded on 25 July.

Eggs obtained in the morning of 10 July were used for the following hatchery

production: *c.* 44,000 eggs were spawned under natural temperature (21.8° C) and sub-samples of *c.* 11,000 floating eggs were placed into each of two black 500-l polyethylene tanks (Tank 1 and Tank 2). Water was exchanged at a rate of 70 l h⁻¹ with filtered seawater at 22.5° C and air was provided at a rate of 600 ml min⁻¹. Hatching was confirmed at 0700 hours on 11 July. Rotifers *Brachionus plicatilis* Müller were fed with a density of 3 ind. ml⁻¹ in the afternoon of the 1st day post hatch (dph), and with a density of 5 ind. ml⁻¹ at 0700 and 1400 hours thereafter until 20 dph. Defrosted green algae *Nannochloropsis* sp. was added to each tank 20 ml at 0800 and 10 ml at 1500 hours to adjust the density to 40,000 cell ml⁻¹. *Artemia* sp. nauplii at 0.1-0.3 ind. ml⁻¹ enriched with nutritional supplement (Marine Gross, Nisshin Marineteck, Japan) were fed from 20 dph until the end of experiment. Three to 10 individuals were sample from both tanks daily until 15 dph, and at 2–5 days intervals thereafter for the measurement of *L_S*. Fish were raised at natural temperature ranging from 21.3 to 25.1° C (23.2 ± 1.0° C, mean ± S.D.) for the first 30 days, then 24.4 to 27.9° C (26.7 ± 1.1° C) up to 50 dph.

MEASUREMENTS OF BEHAVIOURAL ONTOGENY

Cruise and burst swimming speeds were measured every five days starting on 10 dph as previously described by Masuda *et al.* (2002). In this method, a single fish was transferred to a glass container (10–30 cm diameter depending on the size of fish) covered with a black vinyl sheet on its wall and the movement of fish was recorded from above using a video camera (DCR-HC96, Sony, Tokyo, Japan). After recording for

90 s without disturbance, the fish was startled by sound stimuli to elicit burst response. Consistent sound stimuli were produced using a pendulum (a 10 g of steel nut hung by a string) that was released from a distance of 17 cm from the container wall. Preliminary observation revealed that visual stimuli such as casting a shadow or flashing a camera strobe did not induce consistent responses and that a larva did not seem to visually recognize a predator such as jellyfish until sensing the water current made by a jellyfish. Sound stimuli were provided three times at 10-s intervals. This procedure was repeated for 10 individuals. Cruise swimming speed was measured from 10 s of recording before providing the sound stimulus by tracing the movement of the fish using a flexible ruler on a TV monitor. Burst swimming speed was measured only when the fish made a burst start in response to the sound stimulus, and the largest value among the three trials was used for further analysis. The burst swimming speed was defined as the movement in 0.13 s corresponding to four frames of the video recording. The distance was divided by its standard length (L_S) to express speed as $L_S \text{ s}^{-1}$. Responsiveness, defined as the percentage of obvious burst swimming responses against the provided stimuli, was also measured at each date of measurement.

Escape performance exposed to jellyfish was visually observed using a method previously reported by Nakayama *et al.* (2003) and Masuda (2006). Moon jellyfish *Aurelia aurita* were collected off the MFRS by SCUBA diving. They were kept in two 500-l tanks and were used within 1 week after collection. Three actively pulsating *A. aurita* (mean \pm S.D. bell diameter = 82.8 ± 7.5 mm) were put in a 10-l plastic container. A larger tank made it impossible to follow the movement of the smallest larva and thus

this size of container was used. A larva of *E. japonicus* was gently put in this container, and then observations were conducted to measure how long it took for the fish to be captured by *A. aurita*. The observation was conducted for 5 min, and if the fish was not eaten, it was removed and was replaced by another individual. Ten trials were conducted every 5 days starting from 10 dph up to 40 dph (*i.e.* 70 individuals in total). Same individuals of *A. aurita* were used throughout the replicates on each day, after which they were released in the sea.

Behaviour in rearing tanks was also recorded via a video camera as described by Masuda *et al.* (2003) starting on 20 dph with 3-5 days interval up to 50 dph. Two semicircular reflective panels were put on the tank bottom *c.* 5 min prior to recording to produce a clear image contrast. Focus of the video camera was locked at the layer with highest density of larvae, and video analysis was conducted only on well-focused individuals to capture behaviour of fish swimming in nearly two dimensions. Recording was started at 1500 hours and lasted 5 min each day. Water and aeration was stopped while video recording to minimize the effect of current on behaviour.

Three parameters of schooling were defined for video analysis: separation angle (SA), distance to the nearest neighbour (D_{NN}) and separation swimming index (I_{SS}) (Fig. 1). SA and D_{NN} were criteria of parallel orientation and aggregation, respectively, and were calculated on a still frame (Masuda *et al.*, 2003). A fish close to the centre of the video frame was focused on (focal fish), and then the fish closest to the focal fish was defined as the neighbouring fish. The angle between the body axis of the focal fish and the neighbouring fish was measured on the TV monitor using a protractor and was

defined as the SA. On the same frame, three other individuals close to the focal fish were selected then the distance between each fish to the closest individual from each was measured by a ruler. The average of these five measurements was defined as the D_{NN} of this frame. SA and D_{NN} were sampled from 30 frames each separated with a 20-s interval. SA, ranging from 0° to 180° , was expected to be 90° when fish were located in a random direction and was expected to decrease as they developed a parallel orientation. D_{NN} was also expected to decrease as fish aggregated. D_{NN} was divided by L_S to facilitate the comparison among different size groups.

I_{SS} was analysed from the same video frames as SA and D_{NN} measurements with the addition of frames 1 s after these (Fig. 1b). I_{SS} reflects the tendency of parallel swimming that is typical in the early stage of schooling (Masuda *et al.*, 2003). For the measurement, vectors of the focal fish and the neighbouring fish were defined as movement in a 1-s interval. Then the neighbouring fish vector was moved so that its starting point overlaps with that of the focal fish, and the distance of the endings of two vectors was divided by the average length of the two vectors. I_{SS} ranges from 0 to 2 and it is expected to be 1.49 when two neighbouring individuals moved in random directions at random speeds according to the simulation by Nakayama *et al.* (2007).

Routine swimming speed was also measured from video recordings in rearing tanks. The movement of the focal fish in each video frame was traced for 1 s on a TV monitor. The body length of the focal fish was measured on the TV monitor, and the routine speed was expressed as $L_S \text{ s}^{-1}$.

STATISTICAL ANALYSIS

For the inter- and intraspecific comparisons, swimming speed data of *E. japonicus* was divided into three size groups as pre-flexion (3.7–10 mm), post-flexion (10–21 mm) and metamorphosing (21–33 mm) larvae based on the criteria detailed in Fukuhara (1983). Cruise and burst swimming speeds were compared among these three different size groups using the Kruskal-Wallis test followed by the Dunn's test (Zar, 1996). Swimming speeds of *E. japonicus* were then compared to those in *Trachurus japonicus* and *Scomber japonicus* measured using the same methods (Masuda, 2006). Responsiveness was compared among different size groups and species in the same manner. In the analysis of survival against *A. aurita* predation, the Kruskal-Wallis test followed by the Dunn's test were applied to compare different age (and size) of *E. japonicus* larvae. The parameters of schooling behaviour were measured separately in duplicated tanks, log transformed to improve the homogeneity of variance, and were compared among different age groups in each tank using ANOVA followed by the Tukey's test after a Bonferroni correction. SA and I_{SS} in each group were also compared to 90° and 1.49, respectively, by t-test. All calculations for the statistical analysis were conducted using JMP ver. 5.0.1J software (SAS Institute, Cary, NC, USA) except for the Dunn's test (Zar, 1996).

RESULTS

214 Diameters of *E. japonicus* eggs were 1.25 ± 0.07 and 0.64 ± 0.03 mm in long and
215 short axis, respectively ($n = 11$) (Fig. 2). Mean notochord length of hatched larvae was
216 2.80 ± 0.06 mm. Pigmentation of the retina was first confirmed in the evening of 1 day
217 post hatch (dph) and all larvae had pigmented eyes on 2 dph. They attained 5.9 mm on
218 10 dph, 11.0 mm on 20 dph, 21.5 mm on 30 dph, 28.3 mm on 40 dph and 36.5 mm on
219 50 dph (Fig. 2). The growth of *E. japonicus* was fitted with an exponential curve as
220 follows: $L_S = 3.37 \times e^{0.0542\text{dph}}$ ($R = 0.963$).

221 Cruise swimming speed of *E. japonicus* showed allometric development showing
222 $0.5\text{--}3 L_S \text{ s}^{-1}$ in the larval (< 21 mm L_S) stage but they had a much higher value of $2\text{--}7$
223 $L_S \text{ s}^{-1}$ at the metamorphosing stage. Cruise speed in the metamorphosing stage of *E.*
224 *japonicus* was higher than values in the larval stage (Dunn's test, $P < 0.05$; Table I).
225 Cruise speed of *E. japonicus* in $10\text{--}21$ mm L_S was significantly slower than that of
226 *Scomber japonicus* in the same size range. Burst swimming speed also showed an
227 allometric development. Burst speed of metamorphosing *E. japonicus* was significantly
228 faster than smaller (< 21 mm) individuals. Burst speeds of *E. japonicus* larvae were the
229 slowest among the three fish species, and were significantly slower than those of
230 *Trachurus japonicus* for both size ranges. Responsiveness to sound stimuli gradually
231 increased as fish grew, increasing from $43\text{--}50\%$ in $6\text{--}11$ mm L_S larvae to $87\text{--}93\%$ in
232 $17\text{--}26$ mm L_S larvae. Responsiveness of *E. japonicus* was significantly inferior to that
233 of *T. japonicus* for both size ranges (Table I).

234 Larvae of *E. japonicus* smaller than 11 mm L_S were preyed upon by *A. aurita* in
235 150 s on average (Fig. 3). Anti-predator performance gradually improved, although

three out of ten individuals were eaten even when they attained 23 mm L_S . All ten individuals survived 5-min predation trial in 26 mm or larger fish. Survival of *E. japonicus* exposed to *A. aurita* was markedly inferior to that of *T. japonicus* and *S. japonicus* (Masuda, 2006).

Separation angle (SA) gradually decreased in larvae from 15 to 25 mm L_S , indicating that parallel orientation developed during this period (Fig. 4a). Distance to the nearest neighbour (D_{NN}) also decreased in this period, and values for 23 mm L_S fish and larger showed an almost consistent value between 0.7 and 1.0 L_S (Fig. 4b). Decrease of the separation swimming index (I_{SS}) was also remarkable between 15 and 25 mm L_S (Fig. 4c). SAs were significantly smaller than 90° for all fish in the 17 mm L_S size group and larger (t -test, $P < 0.05$; Fig. 4a). I_{SS} were also smaller than 1.49 for all groups at 17 mm L_S and larger (t -test, $P < 0.05$; Fig. 4c). Average routine swimming speed in rearing tanks showed an allometric development from 1.6 L_S s⁻¹ on 20 dph (11 mm L_S) to 5.7 L_S s⁻¹ on 38 dph (28 mm L_S) (Fig. 4d).

DISCUSSION

In rearing tanks, the growth of *E. japonicus*, which attained 28.3 mm L_S in 40 dph, was similar to that reported for wild specimens estimated from otolith growth increments, i.e., attaining *c.* 30 mm L_S in 40 dph (Takahashi *et al.* 2001) or mean growth rates of 0.58 mm d⁻¹ (Takasuka *et al.* 2004) or 0.60 mm d⁻¹ (Hwang *et al.* 2006). The similarity of growth to wild specimens suggests a healthy condition for hatchery-reared

larvae in the present study. Interspecific comparison revealed that the daily specific growth rate of *E. japonicus* was intermediate between *T. japonicus* and *S. japonicus* (Fig. 1). The body form of *E. japonicus* is relatively elongate compared to *T. japonicus* and *S. japonicus*. Therefore growth of body mass in *E. japonicus* would be lower than was expressed in L_S .

A single individual was observed in a limited space for the measurement of cruise swimming, burst swimming, and predation by jellyfish in this study. This method can make use of a limited number of materials and also facilitate comparison among different species of fish larvae reared under different conditions. The drawback is the potential stress on experimental animals. However, fish larvae usually accepted prey items in the small container immediately after transfer, thus indicating that the impact of stress on their behaviour may have been minimal.

Video analyses using single fish revealed that *E. japonicus* larvae are relatively slow in both cruise and burst swimming compared to *T. japonicus* and *S. japonicus*. Hunter (1972) measured the swimming speed of *Engraulis mordax* as $15 L_S s^{-1}$ of burst speed and $1 L_S s^{-1}$ of intermittent swimming and concluded that they are relatively slow swimmers. Fuiman *et al.* (1999) pointed out that slower swimming species such as *E. mordax* and *Clupea harengus* are typically elongate larvae that transform at larger sizes than fast swimmers such as *Sciaenops ocellatus*, *Scomber japonicus* and *Pagrus major* (Temminck & Schlegel). A slow cruise swimming speed would reduce the chance of encountering prey items and thus may induce a relatively slow growth of *E. japonicus*. Although a slow cruise swimming speed may reduce the chance of encountering

predators, slow burst speed should be disadvantageous in avoiding predators once they are encountered (Fuiman & Magurran, 1994).

Average routine swimming speed in rearing tanks gradually increased and the trend corresponded well with that of the cruise swimming speed measured on a single individual in an experimental container. O'Connell (1981) described that the number of red fibers in trunk musculature increased from 2–3 layers at 16 mm L_S to 7–8 layers at 26 mm L_S in *Engraulis mordax*. Similar development of red muscle in *E. japonicus* is likely to have enabled the improvement of cruise and routine swimming observed in the present work. Swimming speed measured in still water, however, tends to be slower than that measured in a chamber with current or in the open ocean (Clark *et al.*, 2005; Leis *et al.*, 2006). Therefore caution should be used when applying absolute values of swimming speeds obtained in laboratory systems to ecological contexts.

Average responsiveness to sound stimuli increased from 43–50% in 6–11 mm L_S to 87–93% in 17–26 mm L_S larvae of *E. japonicus*. Folkvard and Hunter (1986) studied responsiveness of larval *E. mordax* to predation by adult *E. mordax* and juvenile *Scomber japonicus*, and found that 18–48% of 6–13 mm L_S larvae and 70–100% of 15–50 mm L_S larvae responded to attacks by predators. Considering that their measurement was based on the response to live predators and thus some larvae failed to respond before being eaten, the tendency of increased responsiveness in *E. japonicus* during ontogeny was similar to that of *E. mordax*.

Engraulis japonicus were highly vulnerable to jellyfish predation in the present experiment; possible causes of this were low responsiveness, slow burst swimming, and

fragile body surface. Müller (1984) reported that *Clupea harengus* larvae suffer high mortality during blooms of *Aurelia aurita*. Capelin *Mallotus villosus* (Müller) larvae also suffer substantial mortality by *A. aurita* predation (Elliott & Leggett, 1997). Larvae of *E. japonicus*, *C. harengus* and *M. villosus* have transparent and elongate bodies that should be adapted to avoid visual predators, but may not be efficient in avoiding tactile predators such as jellyfish. Baily & Batty (1984) compared predation by *A. aurita* on the yolk-sac larvae of cod *Gadus morhua* L., flounder *Platichthys flesus* L., plaice *Pleuronectes platessa* L. and *C. harengus*, and found that species with smaller larvae (*i.e.*, *P. flesus*) were more vulnerable to capture. They attributed the susceptibility of small larvae to fewer reactions to encounter with *A. aurita*, which is in accordance with the present work. They also suggested that smaller larvae received a higher dose of toxin per unit of body weight. This high-dose susceptibility may also apply to transparent and elongate-bodied larvae. Perhaps *E. japonicus* lack some protection from nematocyst stings on their skin, which *T. japonicus* and *S. japonicus* possess. This may explain why only small larvae of *T. japonicus* and *S. japonicus* were preyed upon, whereas in the present work much larger *E. japonicus* larvae were preyed upon.

The first sign of schooling behavior was observed at 17 mm L_S and schooling was completed at 25 mm L_S . Hunter & Coyne (1982) reported that the *E. mordax* begins schooling at 11–15 mm L_S . This discrepancy in the timing of schooling onset between the two species is unlikely to be due to interspecific differences in morphological development, as both show similar morphological changes in sensory and swimming organs. For example, rod cells in the retina appear at 14 mm L_T (= 12 L_S) and 10 mm L_S

(O'Connell, 1981; Uyan *et al.*, 2006), and guanine deposition is complete at 34 mm L_S and 35 mm L_S in *E. japonicus* and *E. mordax*, respectively (Takahashi & Watanabe, 2004). Hunter & Coyne (1982) conducted behavioural observations in rearing tanks whilst rearing water was being supplied, so that there should have been some water current in their rearing tanks. Fish larvae often show rheotaxis so that they can form school-like aggregations in moving water, which often collapses when the current is stopped (Masuda unpubl. data). Indeed Hunter & Coyne (1982) suggested that the disturbance of changing the water and the resulting fright response induced an early onset of schooling. In any case, in contrast to most fish species that start to show schooling behaviour when they attain the juvenile stage (Masuda & Tsukamoto, 1999), both *Engraulis* species start to form schools prior to metamorphosis. This may imply that the *Engraulis* life history strategy strongly depends on schooling behavior.

The basic formation of buccal lateral line nerves in *E. japonicus* is established by 20 mm SL (Ohshimo, 1999), and then the supraorbital canal walls are completely ossified by 30.8 mm L_T (\approx c. 26 mm L_S) (Uyan *et al.*, 2006) corresponding with the onset of schooling behaviour. This is in agreement with Cahn *et al.* (1968) who suggested that canalization of buccal lateral line facilitates the capability of detecting specific water movement and thus enables parallel orientation in schooling. Ogawa (1967) described *E. japonicus* larvae smaller than 25 mm L_T (\approx c. 22 mm L_S) to have an immature brain form with relatively small cerebelli; this implies that the development of the brain may also be required for the onset of schooling.

Once schooling behavior was established, D_{NN} of *E. japonicus* was about 0.7–1.0

fold L_S . D_{NN} of Spanish mackerel *Scomberomorus niphonius* (Cuvier) measured using the same method was about 1.2–1.5 L_S (Masuda et al., 2003) and 2.2 L_S in Pacific bluefin tuna *Thunnus orientalis* (Temminck & Schlegel) (Torisawa et al. 2007). The difference of D_{NN} is likely to reflect feeding strategy; piscivores like *S. niphonius* and *T. orientalis* feed efficiently on highly mobile prey by expanding their search area, whereas planktivores like *E. japonicus* larvae keep a low D_{NN} so that their school will be less conspicuous without reducing feeding opportunities. Uyan et al. (2004) suggested that the well-developed buccal lateral line system of this species is likely to enable the high manoeuvrability in schooling.

Even though *E. japonicus* larvae are slow swimmers and ideal prey for various piscine and gelatinous predators, their populations seem relatively stable in Japanese coastal waters (Masuda, 2009). This is also the case for congeners in the Mediterranean Sea, where *E. encrasicolus* is the most dominant species in coastal waters (Sabatés et al., 2003). Somarakis et al. (2004) attributed the abundance of *E. encrasicolus* to their high fecundity. *Engraulis japonicus* also have a high fecundity and spawn from early spring to autumn, and they mature in as short as six months (Tsuruta, 1992), which compensates for its short life span (Kawasaki, 1980). This reproductive advantage may allow the *E. japonicus* population to persist even with high predation pressure by jellyfish as well as fishing pressure. This is in contrast to the *Sardinops melanostictus* in which maturation requires one or two years and spawning usually occurs during limited time of year at specific sites (Morimoto, 2003).

Engraulis japonicus larvae are likely to be preyed upon by both piscine and

gelatinous predators. Reductions of piscine predators caused by overfishing may work advantageously to the population of *E. japonicus* at least temporarily. Blooms of jellyfish, however, threaten *E. japonicus* larvae. The threat is even more serious as the trend of the period of jellyfish blooms extends due to the reduced quality of coastal waters as well as the global warming trend (Purcell *et al.*, 2007). Survival of *E. japonicus* larvae exposed to predators under various conditions such as elevated temperature and turbidity requires further research.

Rotifers required for rearing *E. japonicus* were kindly provided by Notojima Station, National Center for Stock Enhancement. The author would like to thank M. Walsh, C. Brown and two anonymous referees for constructive comments on the manuscript. This study was supported by a Grant-in-Aid from Japan Society for the Promotion of Science, STOPJELLY Project from the Agriculture, Forestry and Fisheries Research Council, Japan, and Food and Function Research Center, Nippon Suisan Kaisha, Ltd. The experiments were conducted in accordance with the guidelines of Regulation on Animal Experimentation at Kyoto University.

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Table I. Comparison of cruise swimming speed, burst swimming speed and responsiveness among different size groups, and among the three different fish species

	3.7–10 mm	10–21 mm	21 mm–33 mm
Cruise Speed ($L_S s^{-1}$)			
<i>Engraulis japonicus</i>	1.42 ± 0.74 (23) b	1.80 ± 0.99 (19) b	3.85 ± 1.24 (17) a
<i>Trachurus japonicus</i>	1.75 ± 1.15 (95)	1.65 ± 0.99 (55)	
<i>Scomber japonicus</i>	1.56 ± 0.72 (23)	3.20 ± 1.88 (47)*	
Burst Speed ($L_S s^{-1}$)			
<i>Engraulis japonicus</i>	6.08 ± 4.14 (17) b	9.50 ± 6.89 (16) b	28.4 ± 12.1 (17) a
<i>Trachurus japonicus</i>	18.7 ± 9.3 (87) b*	22.7 ± 7.10 (55) a*	
<i>Scomber japonicus</i>	8.03 ± 3.53 (12) b	15.7 ± 5.58 (35) a*	
Responsiveness (%)			
<i>Engraulis japonicus</i>	50.1 ± 40.0 (23) b	64.9 ± 37.6 (19) ab	88.2 ± 26.2 (17) a
<i>Trachurus japonicus</i>	79.3 ± 32.3 (95) b*	97.6 ± 8.7 (55) a*	
<i>Scomber japonicus</i>	27.5 ± 31.2 (23) b	66.7 ± 42.8 (47) a	

Values with different letters are significantly different among size groups in the same species, and values with an asterisk are significantly larger than that of *Engraulis japonicus* in the same size group (Dunn's test, $P < 0.05$).

Figure captions

Fig. 1. (a) Measurements of separation angle (SA) and the distance to the nearest neighbour (D_{NN}). l_1 is the D_{NN} for the individual F, and so is l_2 for the individuals N₁ and N₂. Average of l_1 , l_2 , l_2 , l_3 and l_4 will be the D_{NN} for this frame. (b) Measurement of the separation swimming index (I_{SS}). Swimming trajectories of neighbouring individuals were expressed as vectors, and the distance between the two vectors d divided by the average length of v_1 and v_2 was defined as I_{SS} .

Fig. 2. Growth (mean \pm S.D.) of *Engraulis japonicus* (black circles: present work) together with *Scomber japonicus* (triangles) and *Trachurus japonicus* (squares) (Masuda, 2006). Data were fitted to exponential curves.

Fig. 3. Developmental changes of avoidance of *Aurelia aurita* by *Engraulis japonicus* (present work), *Scomber japonicus* and *Trachurus japonicus* (Masuda, 2006). Symbols are the same as in Fig. 2. Values without sharing an alphabet letter differ significantly (Dunn's test, $P < 0.05$).

Fig. 4. Developmental changes of three schooling parameter as (a) separation angle, (b) distance to the nearest neighbour, and (c) separation swimming index and (d) development of routine swimming speed in rearing tanks. Open circles (lower case) and closed circles (upper case) represent tank 1 and tank 2, respectively. Values without sharing an alphabet letter differ significantly (Tukey's test, $P < 0.05$).

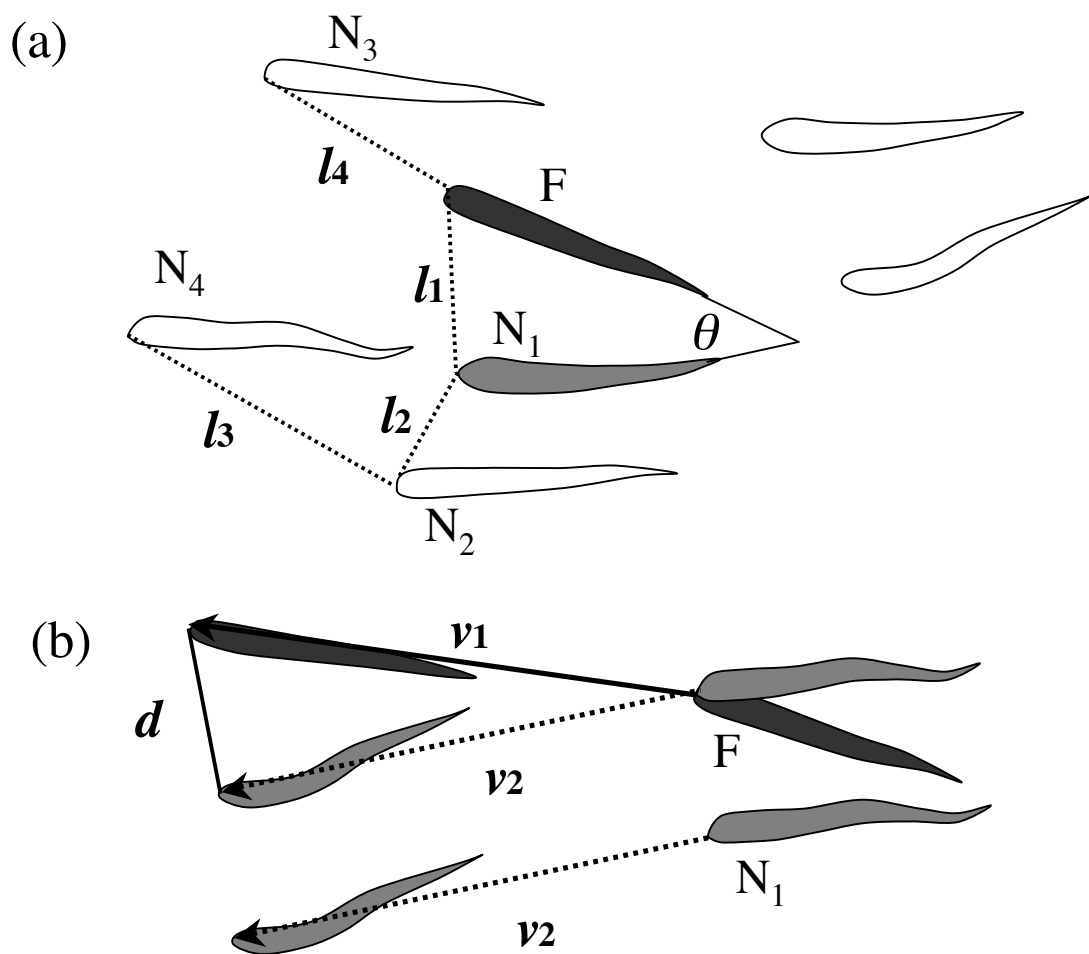


Fig. 1.

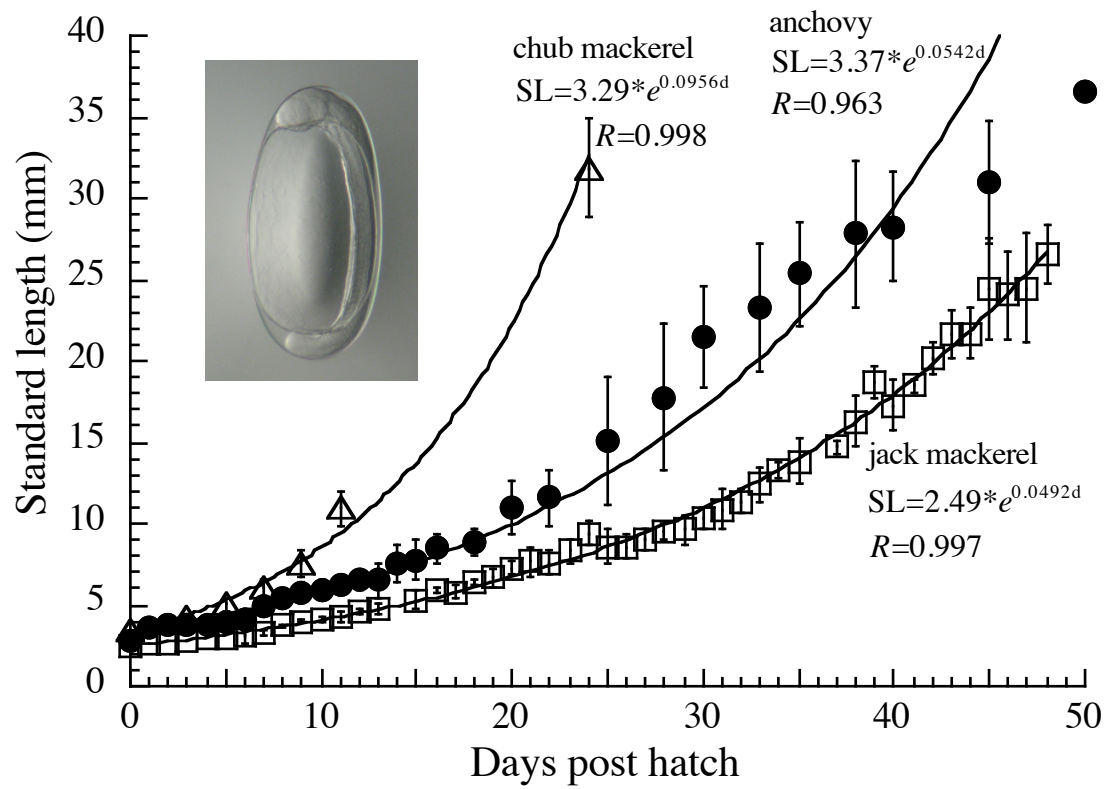


Fig. 2.

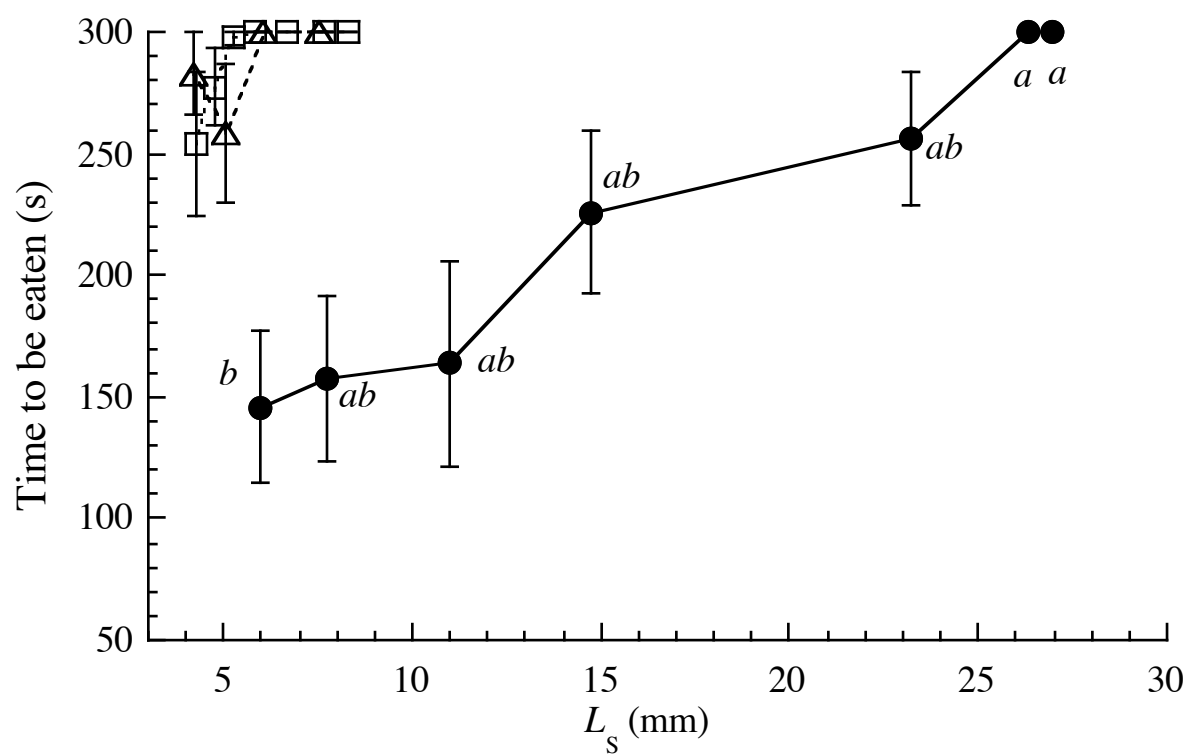


Fig. 3.

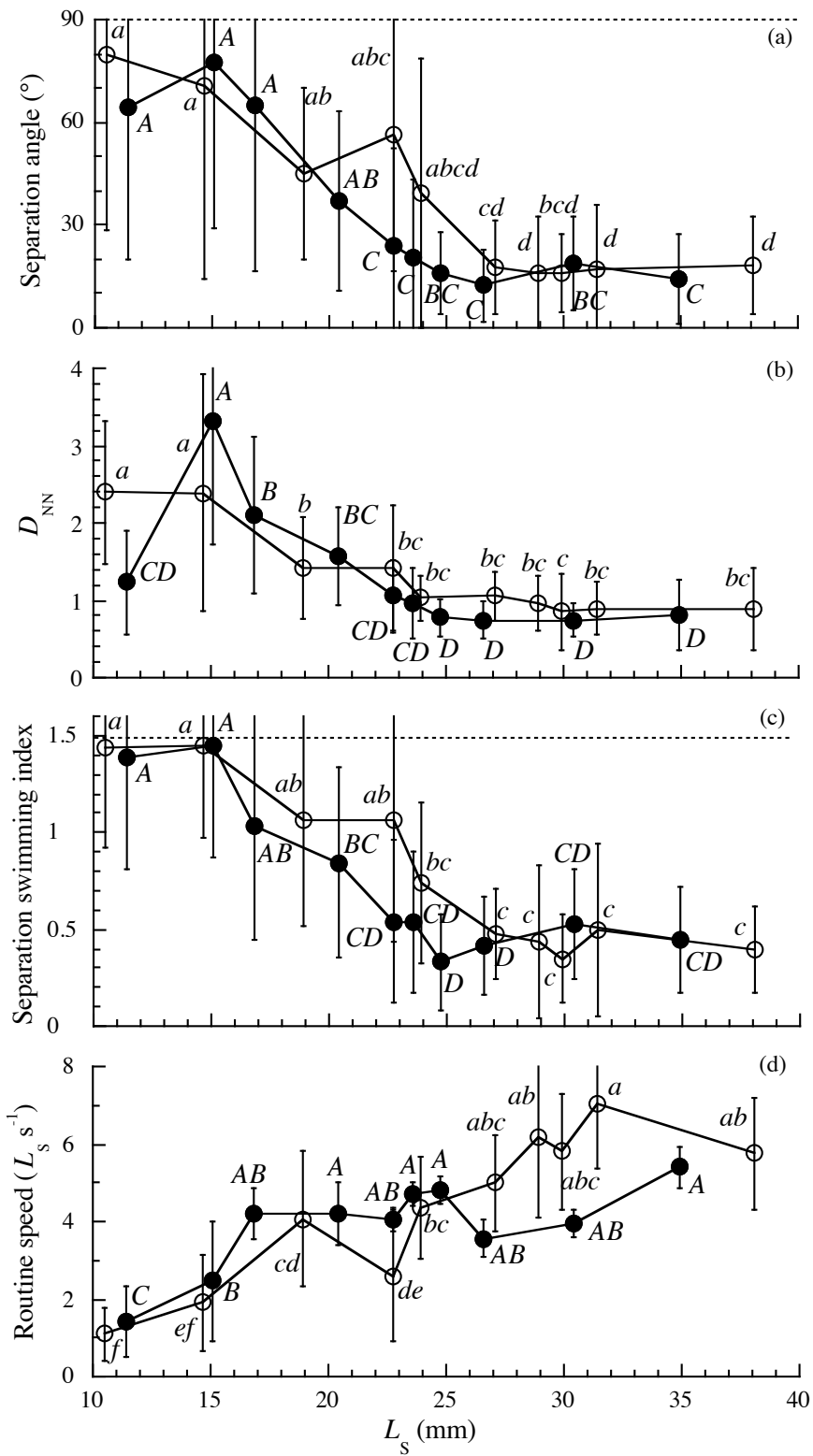


Fig. 4.